

INVITED ARTICLE

Cretaceous and Paleocene fossils reveal an extinct higher clade within Cornales, the dogwood order

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Abstract

Premise: Characterization and phylogenetic integration of fossil angiosperms with uncertain affinities is relatively limited, which may obscure the diversity of extinct higher taxa in the flowering plant tree of life. The order Cornales contains a diversity of extinct taxa with uncertain familial affinities that make it an ideal group for studying turnover in angiosperms. Here, we describe a new extinct genus of Cornales unassignable to an extant family and conduct a series of phylogenetic analyses to reconstruct relationships of fossils across the order.

Methods: Two permineralized endocarps were collected from the Cedar District Formation (Campanian, 82–80 Ma) of Sucia Island, State of Washington, United States. Fossils were sectioned with the cellulose acetate peel technique and incorporated into a morphological dataset. To assess the utility of this dataset to accurately place taxa in their respective clades, we used a series of phylogenetic pseudofossilization analyses. We then conducted a total-evidence analysis and a scaffold-based approach to determine relationships of fossils.

Results: Based on their unique combination of characters, the fossils represent a new genus, *Fenestracarpa washingtonensis* gen. nov. et sp. nov. Pseudofossilization analyses indicate that our morphological dataset can be used to accurately recover taxa at the major clade to family level, generally with moderate to high support. The total-evidence and scaffold-based analyses recovered *Fenestracarpa* and other fossil genera in an entirely extinct clade within Cornales.

Conclusions: Our findings increase the reported diversity of extinct Cornales and indicate that the order's initial radiation likely included the divergence of an extinct higher clade that endured the end-Cretaceous Mass extinction but perished during the Cenozoic.

KEYWORDS

Campanian, fruits, paleobotany, phylogenetic pseudofossilization, total-evidence analysis, turnover

The diversity of extinct higher clades (family level and above) of angiosperms is poorly understood. Reports of fossils with unknown familial and/or ordinal affinities are relatively limited (see Friis et al., 2011, 2018, 2019; Manchester et al., 2018 for examples), and such fossils that are described are rarely integrated in phylogenetic analyses (Sauquet and Magallón, 2018; but see Atkinson, 2018; Friis et al., 2019; Doyle and Endress, 2024). While Early Cretaceous mesofossil floras indicate that the initial radiation of angiosperms resulted in the evolution of extant and extinct higher clades (e.g., Friis et al., 2019), few extinct

higher clades of angiosperms (that are not monotypic) have been identified from Late Cretaceous floras, which obscures angiosperm turnover in deep time and the concomitant macroevolutionary process and patterns that have shaped the diversity of flowering plants seen today (Thompson and Ramírez-Barahona, 2023). To further our understanding on the diversity of extinct higher clades of angiosperms, it is critical to characterize systematically informative fossils (e.g., fruits, flowers, whole plants) with unknown affinities and to subsequently integrate them within a phylogenetic framework with robust morphological datasets. One

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exciting angiosperm group to investigate the diversity of extinct higher clades is the dogwood order, Cornales.

Cornales (600 species) is one of the first asterid (>80,000 species) clades to appear in the fossil record during the Cretaceous (Manchester et al., 2015). At their earliest appearance, near the Turonian-Coniacian boundary (~90 million years ago [Ma]), cornaleans are already diverse and geographically widespread in eastern Asia, western North America, and eastern North America (Takahashi et al., 2002; Atkinson et al., 2018, 2019). The fossil record indicates that these plants continued to diversify throughout the Santonian to Maastrichtian (Knobloch and Mai, 1986; Atkinson, 2016; Stockey et al., 2016; Hayes et al., 2018). Furthermore, molecular divergence time estimates complement the fossil record and indicate that Cornales underwent a rapid radiation during the Late Cretaceous, which resulted in five major extant clades: (1) Cornaceae-Alangiaceae, (2) Curtisiaceae-Grubbiaceae, (3) Nyssaceae-Davidiaceae-Mastixiaceae (NDM), (4) Hydrangeaceae-Loasaceae, and (5) Hydrostachyaceae (Xiang et al., 2011; Fu et al., 2019; Thomas et al., 2021). Most Cretaceous cornaleans, however, are extinct genera that have a combination of characters that preclude assignment to extant families (Takahashi et al., 2002; Atkinson, 2016; Stockey et al., 2016; Atkinson et al., 2017, 2018, 2019), which has been supported by morphological phylogenetic analyses (Atkinson, 2018; Hayes et al., 2018; Atkinson et al., 2019). Thus, it is reasonable to suspect that these fossils potentially belong to at least one extinct higher clade within the order. For assessing the diversity of extinct higher taxa in Cornales, increased sampling and phylogenetic integration of extinct genera with unknown familial affinities is crucial.

For this contribution, we increased the sampling of Cretaceous Cornales by characterizing newly recovered permineralized fruits from the Campanian (~82–80 Ma) of western North America and assigning them to a new genus. Like many other Cretaceous cornaleans, the fruits described in this study have a combination of characters that preclude an assignment to an extant family and major clade. To clarify phylogenetic relationships of these fossils and previously described extinct cornaleans, we first conducted a series of phylogenetic pseudofossilization analyses (described below; see also Matsunaga and Smith, 2021) to assess whether our morphological dataset could recover taxa in accurate positions. We then used this dataset in total-evidence and scaffold-based phylogenetic analyses to reconstruct relationships of fossil Cornales, which reveal that the fruits described in this study and many other genera from the Cretaceous and Paleocene belong to an extinct major clade within the order.

MATERIALS AND METHODS

Fossil specimens

Two permineralized fruits were recovered within calcium carbonate concretions exposed along Henry Point in

Sucia Island State Park, State of Washington, United States. Washington State Parks and Recreation Commission provided a permit to B. A. Atkinson to collect the specimens. The Cretaceous exposures on this island belong to the Cedar District Formation of the Nanaimo Group and is dated to the Campanian according to biostratigraphy and magnetostratigraphy (~82–80 Ma; Ward et al., 2012). Other fossils recovered from Sucia Island include other cornalean fruits, ammonites, terrestrial gastropods, inoceramid bivalves, a theropod femur, *Ceratopetalum* fruits, and winged rosoid fruits (Ward, 1978; Roth, 2000; Ward et al., 2012; Peacock and Sidor, 2015; Atkinson, 2016; Tang et al., 2022, 2023).

Both specimens were revealed by cutting the concretions with a water-cooled diamond-edged saw and sectioned using the cellulose-acetate technique (Joy et al., 1956). Peels were mounted on microscope slides with the xylene-soluble medium Eukitt (O. Kindler GmbH, Freiberg, Germany). The specimens, peels, and microscope slides are housed in the Division of Paleobotany Collections, Natural History Museum and Biodiversity Institute, University of Kansas (KUPB). Accession numbers for slides of fossil specimens are 30975–31187. Specimen images were taken with a Nikon SMZ25 stereomicroscope with a Nikon DS-Fi3 camera attachment (Nikon Corp., Tokyo, Japan) and processed in Photoshop (Adobe, San Jose, CA, USA).

Datasets

To conduct the phylogenetic analyses, we used a combination of morphological and molecular data. We coded the fossil fruits described in this work into a fossil-inclusive character matrix (modified from Atkinson, 2018), which consists of 71 morphological characters and 38 fossil taxa and 48 extant taxa (86 total) (Appendices S1 and S2). Atkinson (2018) chose extant taxa in this matrix based on available morphological data while aiming to capture the range of fruit variation for each family within the order. Extinct taxa were chosen if they were anatomically preserved with detailed descriptions and/or represented oldest members of key groups. The morphological matrix used in this study is available on MorphoBank under Project 5201 (<http://morphobank.org/permalink/?P5201>; O'Leary and Kaufman, 2012) and is also provided in Appendix S2. DNA sequence data for the 48 extant taxa included 26S rDNA, *matK*, and *rbcL* loci, which were downloaded from GenBank (Appendix S3). Sequences were aligned using MAFFT (Katoh and Standley, 2013) in the program AliView (Larsson, 2014). The three loci were chosen because preliminary phylogenetic analyses recovered a drupaceous clade, a similar relationship revealed in the recent study of Thomas et al. (2021), which used over 300 nuclear genes. Thus, we chose to use the aforementioned three loci for our total-evidence analysis. To account for some topological differences between our total-evidence results and Thomas et al. (2021), we ran a phylogenetic analysis using a

constraint tree reflecting the topology from their phylogenetic study (see below).

Phylogenetic pseudofossilization analyses

To test whether the morphological dataset contains a strong enough phylogenetic signal for recovering accurate phylogenetic relationships of fossils, a series of “phylogenetic pseudofossilization” analyses were conducted as detailed by Matsunaga and Smith (2021). More specifically, using a molecular-based constraint tree, a phylogenetic pseudofossilization analysis allows us to assess whether phylogenetic inference of our morphological dataset can accurately place a living taxon back in its original position in the tree after it was pruned from the constraint tree and treated as a pseudofossil via character depletion. First, we constructed the constraint tree using gene sequences from our molecular dataset with Bayesian inference (see below). Note that this tree only includes living taxa; real fossils are not included in the pseudofossilization analyses. A taxon was randomly chosen from each drupaceous genus to be pruned from a copy of the backbone constraint tree using the R (v. 4.1.1, R Core Team, 2023) package *ape* (v. 5.7-1; Paradis and Schliep, 2019), which resulted in a set of nine different trees, each with a single taxon pruned. For imitating fossils with missing data, each pruned taxon (pseudofossil) had some of its scored characters changed to missing in a copy of our morphological matrix unless the original character was coded as inapplicable. The characters selected to be missing are the same characters scored as missing for the new taxon described in this study, which are typical missing characters for most anatomically preserved cornalean fossils (Appendices S2 and S4) (e.g., Atkinson 2016; Atkinson et al., 2017).

For each of the nine pseudofossils, a phylogenetic analysis was conducted using respective backbone constraint trees and versions of the morphological matrix modified for character depletion of the pseudofossil and exclusion of all real fossils. Analyses were conducted using *raxmlGUI* 2.0 (Edler et al., 2021), the graphical interface for the maximum likelihood program *RAXML* (Stamatakis, 2014). The Mk model of morphological evolution was used in each analysis, and 100 bootstrap replicates were generated with each run using a rapid bootstrap with optimized model parameters and branch lengths for the given output tree to assess nodal support (Stamatakis et al., 2008). Herein, we use terms designated by Matsunaga and Smith (2021) whereby the resulting trees from each analysis are referred to as “inferred trees,” the unmodified (original) backbone constraint tree as the “reference tree,” and the extant taxa removed from the backbone constraint tree as “pseudofossils.” To identify the shallowest well-supported node, we traced from the pseudofossil down the tree until we encountered a node with moderate to high bootstrap support (≥ 70 ; Hillis and Bull, 1993; Gernandt et al., 2016) that was accurate to the reference tree topology (Appendices S5 and S6). Note that bootstrap support for morphological data is generally low due to datasets containing low numbers of characters.

Total-evidence phylogenetic analysis

To infer relationships among cornalean taxa, including the taxon described in this paper, a total-evidence analysis was conducted within a Bayesian framework. The morphological and molecular datasets were combined, and the total-evidence analysis was run using *MrBayes* 3.2.7a (Ronquist et al., 2012) on the CIPRES Science Gateway (Miller et al., 2011). We used *PartitionFinder* 2 (Lanfear et al., 2016) with corrected Akaike information criterion (AICc) model selection and a greedy search algorithm to identify best partition schemes and substitution models (Guindon et al., 2010; Lanfear et al., 2012). A GTR + Γ substitution model was assigned for *matK* and *rbcL* loci and GTR + I + Γ for 26S rDNA. The standard model (Mk) for morphological evolution (Lewis, 2001) was assigned to morphological characters. Tree searching was done using two independent runs of Markov chain Monte Carlo with four chains for each run. The analyses ran for 50 million generations, sampling every 5000 generations, with a relative burn-in of 25% (see Appendix S7 for the *MrBayes* block). Average standard deviation of split frequencies was less than 0.02. *Tracer* 1.7 (Rambaut et al., 2018) was used to confirm convergence and ESS values above 200.

Morphological phylogenetic analyses using constraints

We also ran a phylogenetic analysis using our morphological matrix constrained against a topology closely reflecting results from a recent nuclear-based phylogenomic study (Thomas et al., 2021) (see Appendix S8 for the constraint tree topology). The analysis was conducted in *raxmlGUI* 2.0 with the same parameters as our phylogenetic pseudofossilization analyses. The analysis underwent 1000 bootstrap replicates.

Character mapping

Using our morphological matrix and trees recovered from the total-evidence and constrained phylogenetic analyses, we sought to identify potential synapomorphies for clades. The matrix and trees were uploaded to *PAUP** (v. 4.0a; Swofford, 2003) to generate apomorphy lists. Identified potential synapomorphies were then used in comparative anatomy in our discussion (Tables 1 and 2).

RESULTS

Systematic paleontology

Order: Cornales

Family: incertae sedis

Genus: *Fenestracarpa* gen. et sp. nov. Nguyen & Atkinson

Species: *F. washingtonensis* sp. nov. Nguyen & Atkinson

Locality: E.V. Henry Point, Fossil Bay, Sucia Island, Washington, USA.

Stratigraphy and age: Cedar District Formation, early-middle Campanian (~82–80 Ma).

Generic diagnosis: Endocarps thick walled, woody; smooth exterior surface. Locules ellipsoidal to subtriangular, each associated with an apically opening, dorsal germination valve. Valves short, composed of isodiametric sclereids. Inner endocarp of circum-locular fibers. Outer endocarp of isodiametric and elongated sclereids. Vascular bundles restricted to septum periphery for most of endocarp length, transverse septa near apex. One apically attached seed per locule with copious endosperm and raphe ventral in locule.

Specific diagnosis: Endocarps at least 2.9 mm long, between 2.3–3.1 mm wide. Locules 3 to 4 in number. Inner endocarp multiseriate. Vascular bundles small, up to 33 μ m in diameter. Uniseriate layer of distinct cells surrounding embryo cavity.

Holotype: 19233 A.

Paratype: 19238 I bot.

Repository: University of Kansas Biodiversity Institute.

Etymology: The generic epithet *Fenestracarpa* (-carpa = fruit) refers to the holotype's window-like (*Fenestra*-) appearance in cross section. The specific epithet refers to Washington, where the fossils were collected.

Description: *Fenestracarpa washingtonensis* is represented by two woody endocarps. The apices of both specimens were lost in the saw cut, but based on the number of peels, the endocarps are at least 2.9 mm long and are 2.3–3.1 mm wide. Endocarps are relatively smooth, lacking conspicuous ridges and furrows (Figure 1A, B). Fruits are tri- to tetralocular (Figure 1A, B). Locules are ellipsoidal to subtriangular in shape in cross section (Figure 1A, B, E). Two locules of specimen 19233 A contain abnormal cellular contents (Figure 1A, C). Apically opening, thick, dorsal germination valves are associated with each locule and are short, extending roughly between one-third and one-half the length of the fruit (Figure 1C, D). Septa are thick and intersect to form a wide central axis (Figure 2A, B).

The endocarp tissue is sclerenchymatous throughout and composed of two distinct tissue zones. There is an outer endocarp made of several layers of sclereids and a multi-seriate inner endocarp (sensu Morozowska and Wysakowska, 2016) consisting of circum-locular fibers seen in the valves, septa, and central axis (Figure 1E, F). Outer endocarp tissue in the valves consist of isodiametric sclereids (Figure 1C, D). Outer endocarp tissue of the central axis and septa are comprised of a mixture isodiametric and elongated sclereids (Figure 2A, B).

Vascular bundles are mostly restricted to the septum periphery (Figure 2C) and, near the apex of the fruits, transverse the septa toward the ovules (Figure 2E). This vascular pattern is considered “transseptal” sensu Eyde (1963, 1967; see also Figure 7A of Atkinson, 2016). There are no vascular bundles located in the central axis (Figure 2A). Vascular bundles are small, approximately

33 μ m in diameter and made of approximately 15 cells (Figure 2D).

There is one presumably apically attached seed per locule (Figure 2F, G). The raphe is located on the ventral side of the endocarp, adjacent to the central axis (Figure 1E). Endosperm is copious, taking up most of the locule (Figure 2F, G). The embryo cavity is surrounded by tissue that is one cell layer thick (Figure 2G).

Phylogenetic pseudofossilization analyses

Results of the phylogenetic pseudofossilization analyses are illustrated in Figure 3. All nine pseudofossil taxa were recovered in the correct major clade, and seven were recovered in the correct family. Moreover, pseudofossil *Cornus volkensii* was recovered as sister to *C. eydeana*, indicating accurate placement at the subgeneric level (*Cornus* subg. *Cornus*). Pseudofossil *Alangium javanicum* was placed in a relatively more nested position, sister to *A. villosum*. Pseudofossil *Camptotheca acuminata* was recovered within its respective family Nyssaceae but nested within *Nyssa*. Notably, our pseudofossilization analyses recovered four pseudofossils (*Curtisia dentata*, *Grubbia tomentosa*, *Nyssa sylvatica*, and *Mastixia pentandra*) in their original position as reflected in the reference tree. Two pseudofossils were recovered in the wrong families: *Davidia involucrata* and *Diplopanax stachyanthus*. Pseudofossil *Davidia involucrata* was nested within Mastixiaceae, sister to *Diplopanax stachyanthus*, and pseudofossil *Diplopanax stachyanthus* was recovered as sister to *Davidia involucrata* in Davidiaceae (Figure 3).

Eight of the nine pseudofossil taxa had their shallowest well-supported node within their respective major clade (Figure 3). Five taxa had their shallowest well-supported node at the most recent common ancestor (MRCA) of their respective major clades: *Alangium javanicum* (Cornaceae-Alangiaceae), *Camptotheca acuminata* (NDM), *Davidia involucrata* (NDM), *Mastixia pentandra* (NDM), and *Diplopanax stachyanthus* (NDM) (see Appendices S5 and S6 for individual inferred trees). The shallowest well-supported node for pseudofossil *Nyssa sylvatica* was at the *Nyssa* crown node. The MRCA of the cornelian cherry (*Cornus* subg. *Cornus*) clade was the shallowest well-supported node for pseudofossil *Cornus volkensii*. The only pseudofossil taxon without a well-supported node within its respective major clade was *Curtisia dentata*, whose shallowest well-supported node was the MRCA of the Cornaceae-Alangiaceae and Curtisiaceae-Grubbiaceae clade.

Phylogenetic analyses

Our Bayesian total-evidence analysis recovered two clades: one comprising cornaleans with capsular fruits (Hydrangeaceae, Loasaceae, and Hydrostachyaceae; PP = 0.86) and

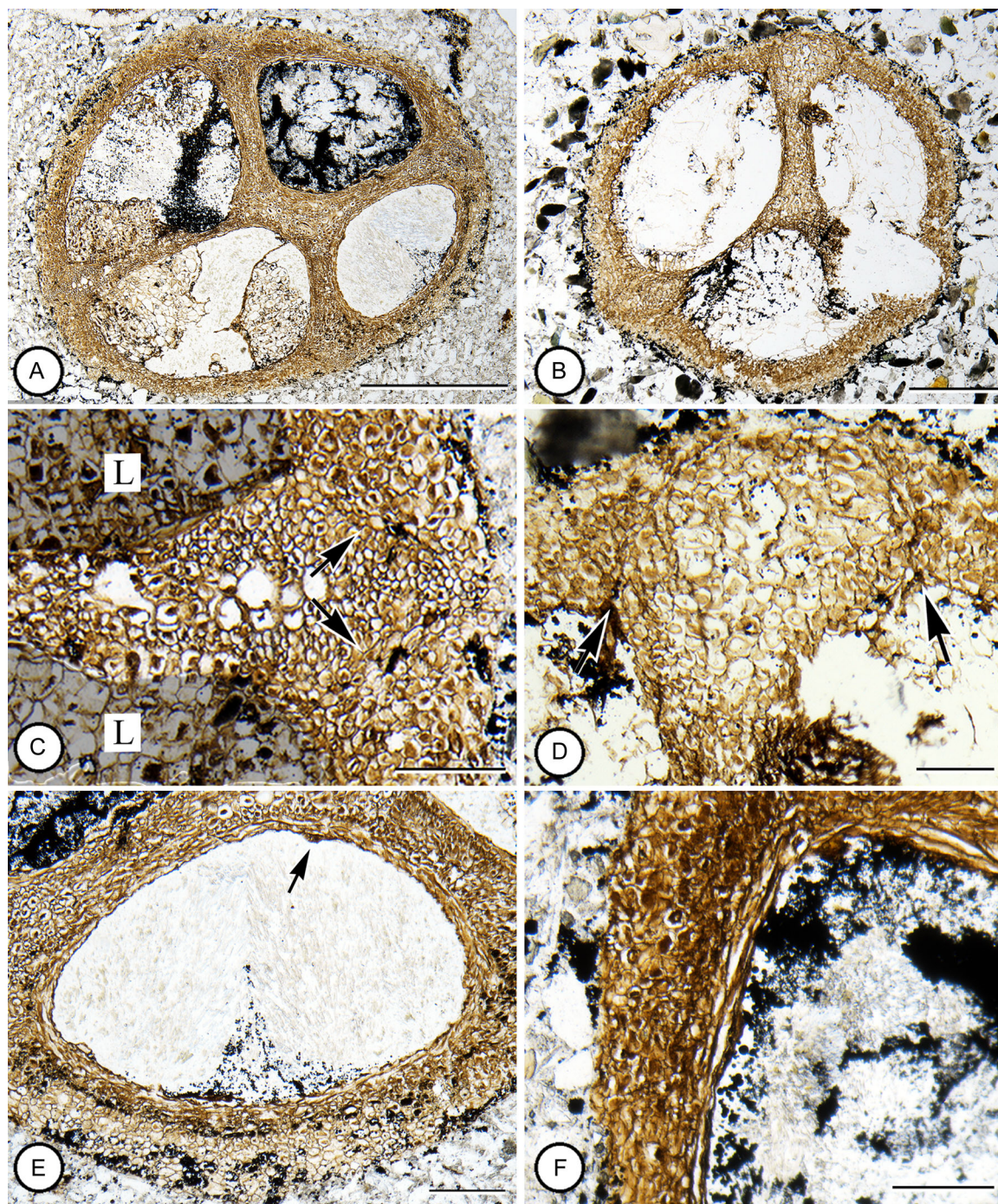


FIGURE 1 *Fenestracarpa washingtonensis* gen. et sp. nov. (A) Oblique cross section of tetralocular endocarp. Note abnormal cellular contents in left two locules. Holotype 19233 A. #14. Slide accession no. 30988. Scale bar = 1.0 mm. (B) Cross section of trilocular endocarp. Paratype 19238 I bot. #28. Slide accession no. 31172. Scale bar = 500 μ m. (C) Cross section of endocarp showing germination valves and their sutures (arrows) adjacent to each side of the septum. Locules (L) and their contents are slightly shaded to increase contrast. Holotype 19233 A. #14. Slide accession no. 30988. Scale bar = 150 μ m. (D) Cross section of septum near endocarp periphery showing germination valves and their sutures (arrows) on each side. Paratype 19238 I bot. #28. Slide accession no. 31172. Scale bar = 100 μ m. (E) Cross section showing one ventral raphe (arrow) and multiserial inner endocarp layer of circum-locular fibers. Holotype 19233 A. #14. Slide accession no. 30988. Scale bar = 200 μ m. (F) Cross section of inner endocarp layer. Holotype 19233 A. #14. Slide accession no. 30988. Scale bar = 100 μ m.

the other consisting of cornaleans with drupaceous fruits (Nyssaceae, Davidiaceae, Mastixiaceae, Cornaceae, Alangiaceae, Curtisiaceae, Grubbiaceae, and extinct taxa with drupaceous fruits; PP = 0.89) (Figure 4). Within the capsular

clade, Hydrangeaceae and Hydrostachyaceae formed a monophyletic group sister to Loasaceae. The only fossil included in the capsular clade, *Hydrangea knowltonii*, was recovered in Hydrangeaceae.

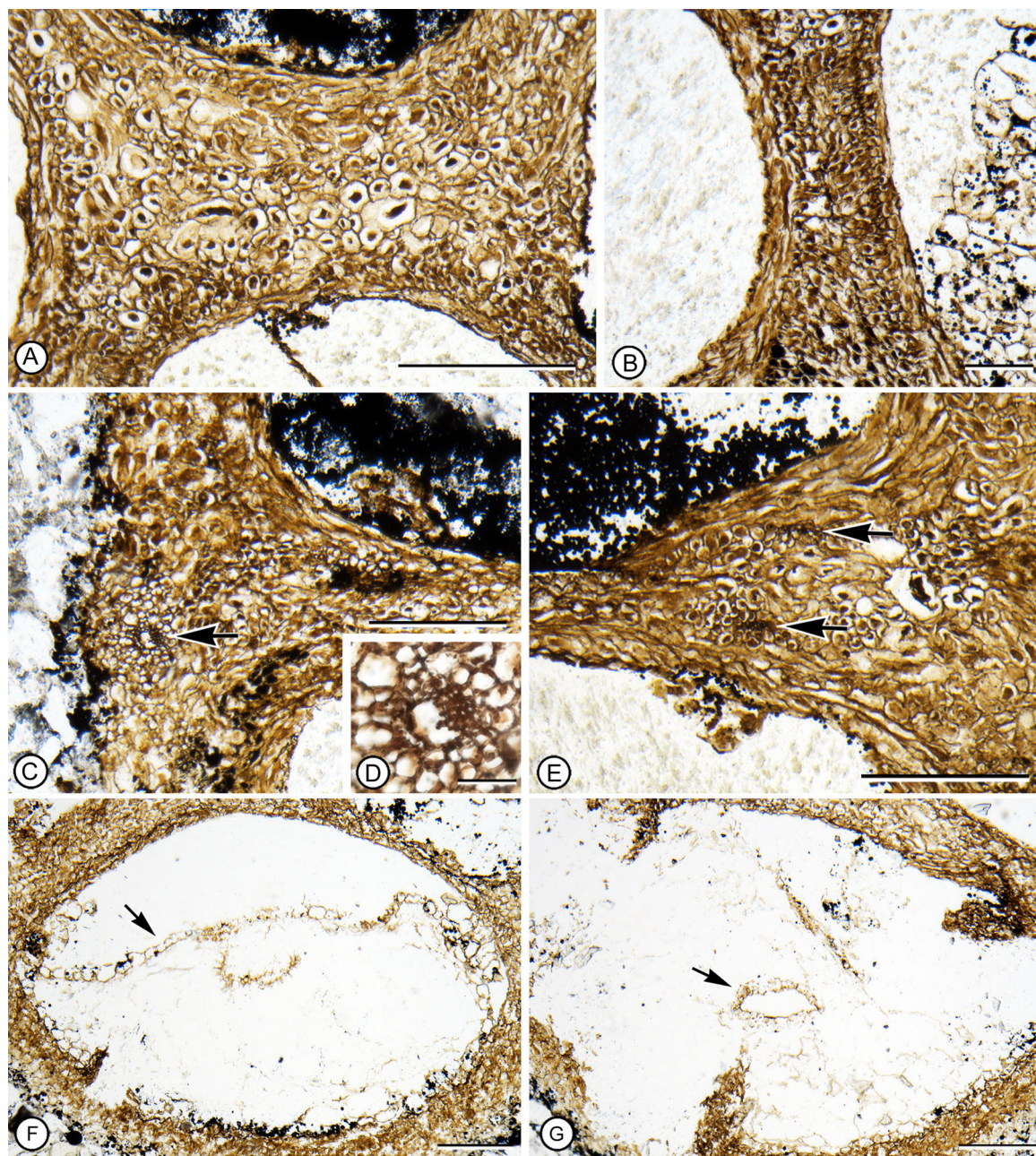


FIGURE 2 *Fenestracarpa washingtonensis* gen. et sp. nov. (A) Cross section of central axis showing isodiametric and elongated sclereids. Note the lack of vascular bundles. Holotype 19233 A. #14. Slide accession no. 30988. Scale bar = 250 μ m. (B) Cross section of septum showing isodiametric sclereids and inner endocarp layers of circum-locular fibers. Note the lack of vascular bundles. Holotype 19233 A. #14. Slide accession no. 30988. Scale bar = 100 μ m. (C) Cross section of septum near endocarp periphery showing isodiametric and elongated sclereids and one vascular bundle (arrow). Holotype 19233 A. #25. Slide accession no. 30999. Scale bar = 200 μ m. (D) Close-up of vascular bundle in C showing xylem and potential phloem gap. Holotype 19233 A. #25. Slide accession no. 30999. Scale bar = 30 μ m. (E) Cross section of septum near endocarp periphery and closer to the apex showing isodiametric and elongated sclereids and two vascular bundles (arrows) transversing the septum. Holotype 19233 A. #75. Slide accession no. 31049. Scale bar = 200 μ m. (F) Cross section of locule containing one seed showing outer endosperm layer (arrow). Paratype 19238 I bot. #39. Slide accession no. 31176. Scale bar = 200 μ m. (G) Cross section of locule containing one seed with embryo cavity (arrow). Paratype 19238 I bot. #77. Slide accession no. 31181. Scale bar = 200 μ m.

Within the drupaceous group, the extant major clades Cornaceae-Alangiaceae, Curtisiaceae-Grubbiaceae, and NDM were recovered. Families in each major clade were monophyletic. Moreover, with the exception of *Amersenia obtrullata*, all fossils that have been previously assigned to these families were recovered in those families.

Our analysis of cornalean phylogenetic relationships recovered a clade comprising entirely of extinct taxa that is sister to the Curtisiaceae-Grubbiaceae clade. Posterior support for this clade was not high (PP=0.68), which is most likely due to frequent topological changes among fossils. With the exception of *Amersenia obtrullata* from the

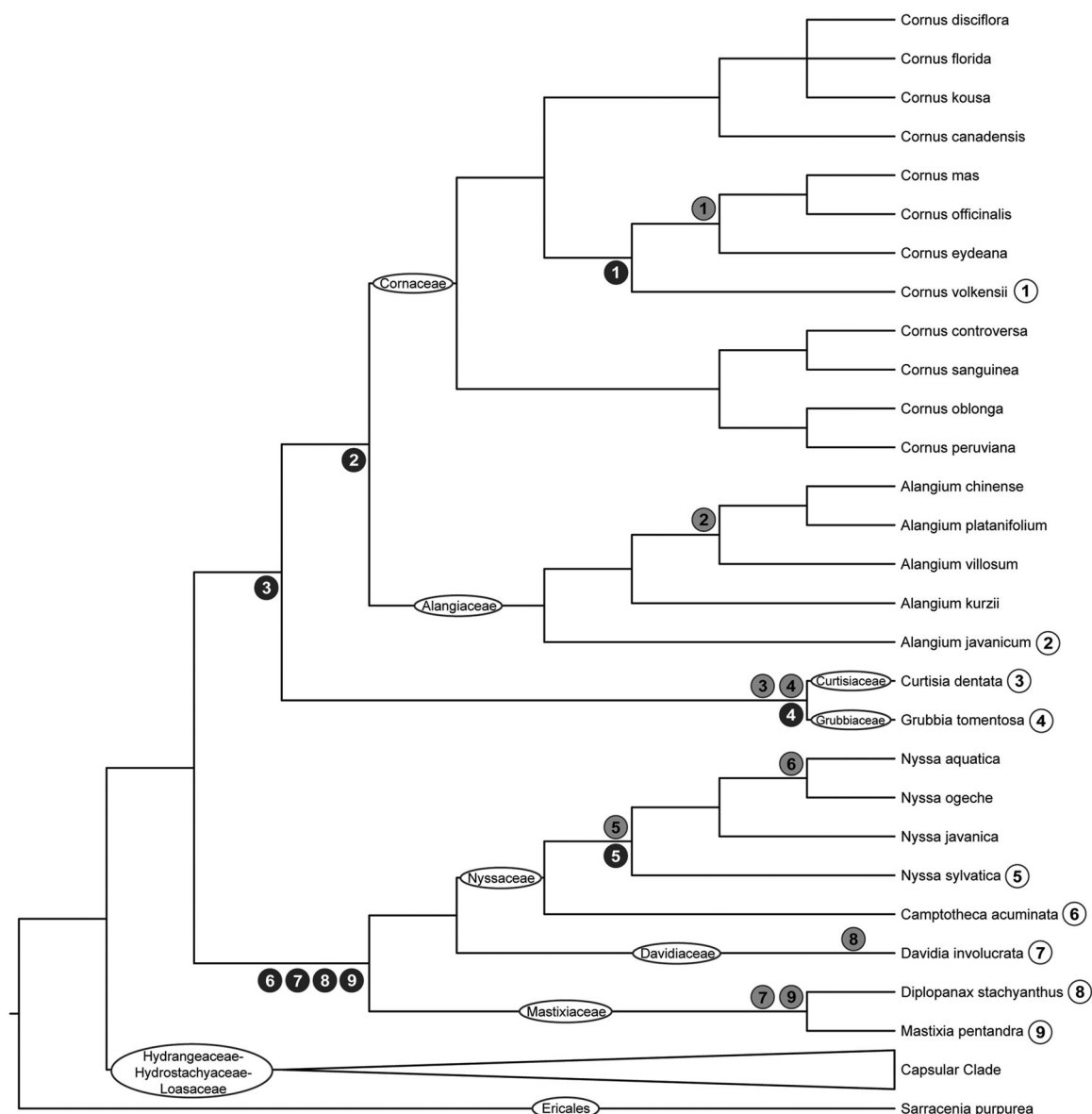


FIGURE 3 Reference tree of the phylogenetic pseudofossilization analyses used to summarize results. Capsular clade (clade including Hydrangeaceae, Hydrostachyaceae, and Loasaceae) is shown collapsed since no pseudofossilization was done on any taxa from that clade. Numbers in white circles next to tips indicate taxa chosen for pseudofossilization analyses. Corresponding numbers in gray circles above branches represent the clade in which the pseudofossil version of that taxon was placed; corresponding numbers in black circles below branches represent the shallowest well-supported node accurate to the reference tree topology. Families and outgroup order (Ericales) denoted by ovals on branches.

Paleocene, this clade consisted of Cretaceous taxa. At the base of this clade is a polytomy comprising *Sheltercarpa vancouverensis*, *Hironia fusiformis*, *Eydeia vancouverensis*, *Eydeia hokkaidoensis*, *Edencarpa grandis*, “Drumheller Fruit 1” (Serbet, 1997; referred to as *Davidia* in Manchester et al., 2015), and a subclade of other fossil taxa. This subclade consisted of *Obamcarpa edenensis*, *Eydeia jerseyensis*, “Drumheller Fruit 2” (Serbet, 1997; referred to as *Nyssa* by Manchester et al., 2015), *Suciicarpa starrii*, *Suciicarpa xiangae*, and *Fenestracarpa*, which was sister to *Amersenia obtrullata* (Figure 4).

Similar to our total-evidence results, the constrained analysis recovered the same extinct clade sister to the

Curtisiaceae-Grubbiaceae clade, although support still remained low (17% bootstrap support for the sister relationship; 12% bootstrap support for the fossil clade). Relationships within the clade were similar to our total-evidence analysis with *Amersenia*, *Fenestracarpa*, *Obamcarpa*, *Eydeia jerseyensis*, both *Suciicarpa* species, and Drumheller fruit 2 in a more nested clade (Figure 5).

Character mapping

For mapping of all characters across all nodes of both trees, see Appendix S9. Table 2 summarizes selected identified

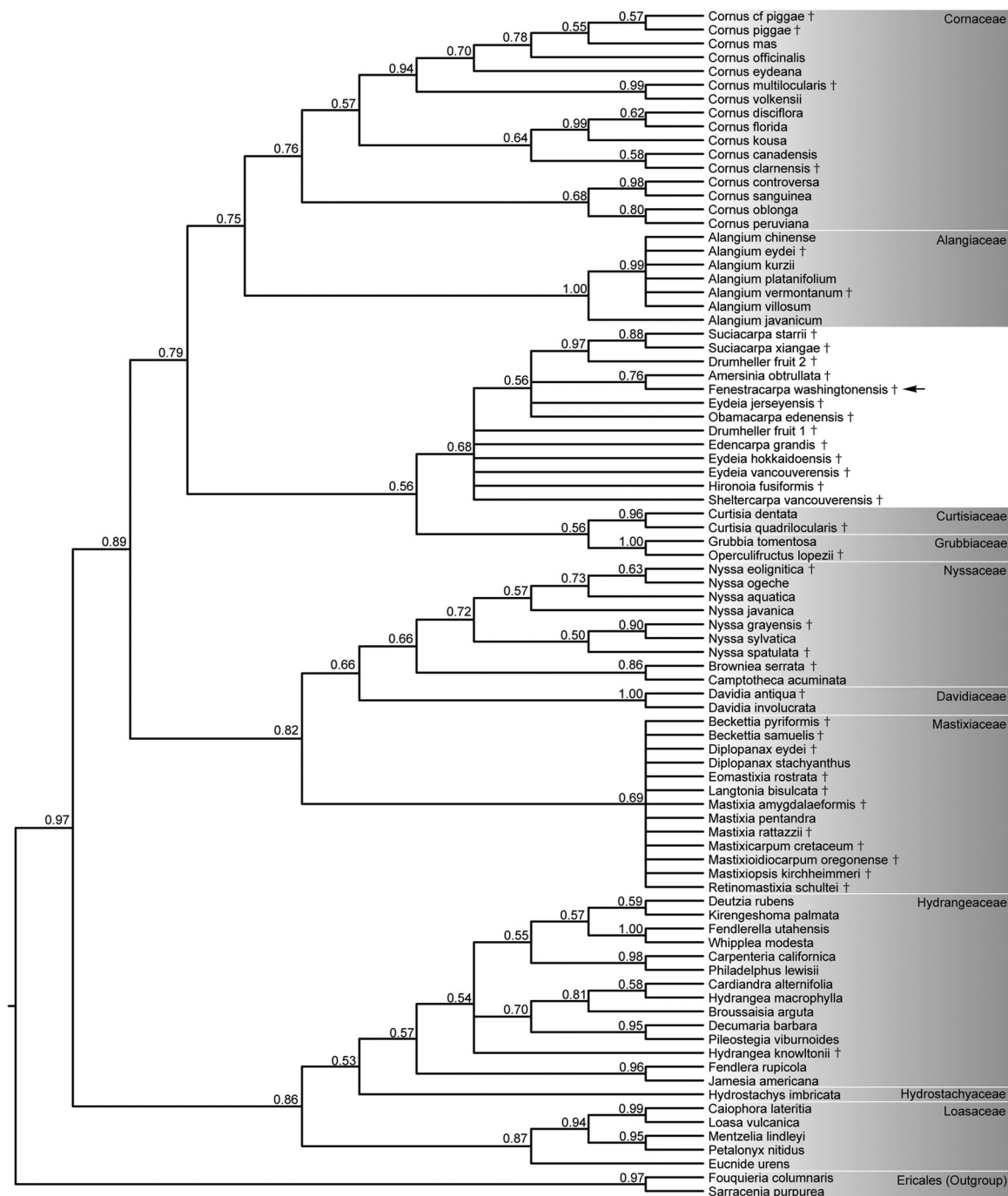


FIGURE 4 Majority rules consensus tree from Bayesian analysis of fossil-inclusive morphological and molecular datasets showing relationships within Cornales. Numbers above nodes denote posterior support. Daggers (†) denote extinct taxa. Arrow denotes fossil species described in this paper. Extant families are shaded in grey.

apomorphies for major clades of drupaceous Cornales. Characters in the apomorphy lists that were scored for most taxa in a clade were selected for our discussion. Under the topology from our total-evidence analysis, PAUP* identified indehiscent fruits, no symplicate zone, thick and woody endocarps, no vascular bundles in the central axis, no persistent calyx/tepale lobes, one apically attached ovule per locule, and a smooth seed coat surface as apomorphies for

the drupaceous clade (Appendix S9). The identified apomorphies for the fossil clade were endocarps with an acuminate apex, elongated sclereids in the central axis and septa, and vascular bundles in longitudinal rows in the septa (Table 2). For the NDM clade, apomorphies included an absence of isodiametric sclereids in the central axis, septa, and gemination valves. Apomorphies for the Cornaceae-Alangiaceae clade included the presence of exterior grooves

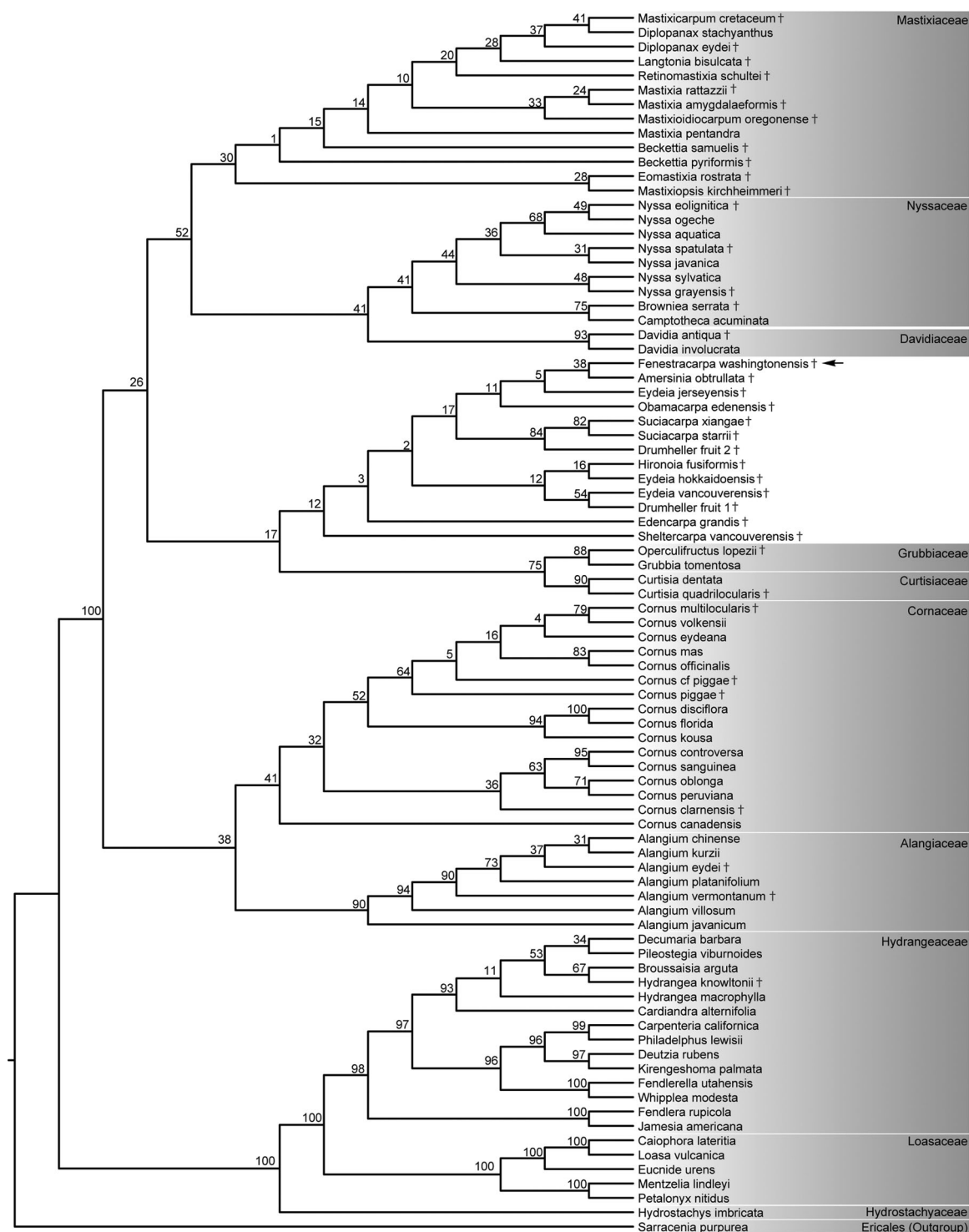


FIGURE 5 Phylogenetic tree from maximum likelihood analysis of fossil-inclusive morphological dataset constrained against a topology reflecting the phylogenomic analysis by Thomas et al. (2021). Numbers above nodes denote bootstrap support. Daggers (†) denote extinct taxa. Arrow denotes fossil species described in this paper. Extant families are shaded in grey.

on the septa and seeds with a lateral/dorsal raphe position. Curtisiaceae-Grubbiaceae had vascular bundles in the central axis, a non-elongate endocarp shape, and no ridges on the exterior surface of germination valves or dorsal surface as identified apomorphies (Table 2).

Similar apomorphies were identified under the constraint tree topology (Appendix S9). A fleshy mesocarp at maturity was an additional apomorphy identified for the drupaceous clade. Except for vascular bundles arranged in longitudinal rows in the septa, the same apomorphies were

identified for the fossil clade (Table 2). For the NDM clade, fibers in the central axis, septa, and germination valves were additional identified apomorphies. Absence of a locule lining was an additional apomorphy identified for the Cornaceae-Alangiaceae clade. The same apomorphies were identified for the Curtisiaceae-Grubbiaceae clade except for the lack of ridges on the exterior surface of germination valves or dorsal surface (Table 2).

DISCUSSION

Fruit diversity in Cornales and assignment of *Fenestracarpa* to the order

Fruits are systematically and phylogenetically informative within Cornales (Wilkinson, 1944; Eyde, 1963, 1967, 1968, 1988; Yembaturova et al., 2009; Manchester et al., 2010; Atkinson, 2016; Stockey et al., 2016; Hayes et al., 2018; Atkinson et al., 2017, 2018, 2019). Broadly, there are two fruit types within the order. The first type is a fleshy drupaceous fruit with a thick woody endocarp that has apically opening germination valves (or operculum as in Grubbiaceae; Hayes et al., 2018) and a single seed per locule with a smooth seed coat, which characterizes seven families within three major clades: Clade 1, Cornaceae and Alangiaceae; Clade 2, Curtisiaceae and Grubbiaceae; and Clade 3, Nyssaceae, Davidiaceae, and Mastixiaceae (NDM) (Eyde, 1963, 1967, 1968, 1988; Fan and Xiang, 2003; Xiang et al., 2002, 2011; Atkinson, 2018; Fu et al., 2019; Thomas et al., 2021). The second fruit type is a dry capsule with many seeds per locule that lack a thick woody endocarp, which is diagnostic of three families in two major clades within Cornales: Clade 4, Hydrangeaceae and Loasaceae; and Clade 5, Hydrostachyaceae (Brown and Kaul, 1981; Leins and Erbar, 1988, 1990; Roels et al., 1997; Hufford, 1997, 2001; Weigend et al., 2004; Xiang et al., 2011; Morozowska et al., 2012; Thomas et al., 2021). The combination of characters in the fruits of *Fenestracarpa* are diagnostic of drupaceous Cornales.

Several important characters are informative for distinguishing genera, families, and major clades for cornaleans with drupaceous fruits, which are shown in Table 1 and discussed below. Characters relating to endocarp histology, valve length, vasculature, and ovule raphe positions hold particular systematic importance (Wilkinson, 1944; Eyde, 1963, 1967, 1988; Atkinson, 2016; Stockey et al., 2016) with each major drupaceous clade having diagnostic combinations of such characters (Table 1). Important endocarp histological characters include the presence or absence of isodiametric sclereids, elongated sclereids (referred to as rice-grain shaped sclereids in Manchester et al., 2010), and/or fibers (Eyde, 1963, 1988; Yembaturova et al., 2009). In addition, the presence or absence of an inner endocarp (sensu Morozowska and Wysłowska, 2016), is another informative character, especially for distinguishing (sub)genera. The inner endocarp is a multiseriate layer typically consisting of

circum-locular fibers that are horizontally elongated around the circumference of the locule (including areas of the valve and septa/ventral wall); this tissue should not be confused with longitudinally elongated cells in the uni- to biseriate locule lining. The outer endocarp is the remaining tissue of the endocarp that surrounds the inner endocarp. The outer endocarp is considered to be similar to the ground tissue of an endocarp that lacks an inner endocarp (Atkinson, 2018).

The vascular pattern within the endocarp is one of the most studied and significant features of drupaceous cornaleans, especially for families and major clades (Wilkinson, 1944; Eyde, 1967; Yembaturova et al., 2009; Atkinson, 2016, 2018). Drupaceous cornaleans often lack a central vascular bundle, which is relatively uncommon in flowering plants (Eyde, 1967). The only exception to this is the Curtisiaceae-Grubbiaceae clade (Smith and Smith, 1942; Manchester et al., 2007; Yembaturova et al., 2009), which is unique among extant drupaceous cornaleans by having a vascular bundle in the center of the central axis (see Table 1). Endocarps of the Cornaceae-Alangiaceae and NDM clades are either vascularized by bundles restricted to the outer peripheries of the septa (transseptal vasculature) or by longitudinal rows of bundles distributed throughout the septa or ventral wall (Eyde, 1963, 1967, 1968). Typically, differences of at least two of the above important characters help distinguish endocarps between major clades and families (e.g., Atkinson, 2016; Atkinson et al., 2017, 2018).

Due to the presence of woody endocarps with apically opening germination valves, transseptal vasculature, and a single apically attached seed per locule, *Fenestracarpa* is assignable to Cornales; however, as discussed below, fruits of this extinct genus have a unique combination of characters that preclude it from being assigned to any extant family or major clade (Table 1), which is supported by our phylogenetic analyses (Figures 4 and 5). For instance, *Fenestracarpa* endocarps have elongated sclereids and an inner endocarp and lack a central vascular bundle, while endocarps in the Curtisiaceae-Grubbiaceae clade lack elongated sclereids and an inner endocarp and have a central vascular bundle. Due to these differences and the results of our phylogenetic analyses, we suggest that *Fenestracarpa* cannot be assigned to this extant major clade.

Fruits of the Cornaceae-Alangiaceae clade are characterized by the presence of endocarps with elongate germination valves that run most of the fruit length (Eyde, 1968, 1988; Atkinson, 2018;). Moreover, the endocarps within this clade are composed of isodiametric sclereids and have transseptal vasculature (Wilkinson, 1944; Eyde, 1968, 1988; Stockey et al., 2016). It is worth noting that *Cornus* subg. *Cornus* have an inner endocarp layer (Morozowska et al., 2013, 2021; Morozowska and Wysłowska, 2016; Table 1). In addition, a potential synapomorphy for this major clade is that the raphes of the ovules/seeds are in a dorsal/lateral position while in all other cornalean taxa they appear to be mostly in a ventral position (Smith and Smith, 1942; Eyde 1963, 1968, 1988; Yembaturova et al., 2009; Tables 1 and 2). While *Fenestracarpa* has endocarps with transseptal vasculature and an inner

TABLE 1 Comparison of endocarp structure among similar fossil and extant cornalean species. XS, cross section.

Taxon	Exterior					Septum histology	Histology of central axis	Valve histology	Inner endocarp*	Endocarp vasculature	Raphe position
	Age	Locule no./fruit	Locule shape	ridge(s) on valve	Valve length						
<i>Fenestracarpa washingtonensis</i>	Campanian	3–4	Subtriangular to ellipsoidal	Absent	Short	Isodiametric, elongate sclereids	Isodiametric, elongate sclereids	Isodiametric sclereids	Present	Transseptal	Ventral
<i>Obamacarpa edenensis</i>	Coniacian	3	Subtriangular to ellipsoidal	Absent	Short	Isodiametric sclereids	Isodiametric sclereids	Isodiametric sclereids	Present	Longitudinal rows in septa	Ventral
<i>Edencarpa grandis</i>	Coniacian	3–4	Subtriangular to ellipsoidal	Absent	Elongate	Isodiametric sclereids	Isodiametric sclereids	Isodiametric sclereids	Absent	Longitudinal rows in septa	?
<i>Eydeia hokkaidoensis</i>	Santonian	4–(5)	Subtriangular to ellipsoidal	Present	Elongate	Isodiametric, elongate sclereids	Elongate sclereids	Isodiametric sclereids	Absent	Longitudinal rows in septa	Ventral
<i>Eydeia vancouverensis</i>	Coniacian	3–4–(5)	Subtriangular to ellipsoidal	Present	Elongate	Isodiametric, elongate sclereids	Elongate sclereids	Elongate, isodiametric sclereids	Absent	Longitudinal rows in septa	Ventral
<i>Eydeia jerseyensis</i>	Turonian	3	Subtriangular to ellipsoidal	Present	Short	Isodiametric sclereids	Isodiametric sclereids	Isodiametric sclereids	Present	Longitudinal rows in septa	?
<i>Hironoia fusiformis</i>	Coniacian	3–(4)	Subtriangular	Present	Elongate	Elongate, isodiametric sclereids	Elongate, isodiametric sclereids	Isodiametric sclereids	Present	Central	Ventral
<i>Suciacarpa starrii</i>	Campanian	4	Crescent-shaped	Absent	Short	Elongate sclereids, secretory cavities	Elongate sclereids	Isodiametric sclereids, secretory cavities	Present	Longitudinal rows in septa	Ventral
<i>Suciacarpa xiangae</i>	Campanian	4	Crescent	Absent	Short	Fibers, secretory cavities	Fibers, secretory cavities	Isodiametric sclereids & secretory cavities	Present	Longitudinal rows in septa	?
<i>Amersinia obtrullata</i>	Paleocene	3–(4)	Subtriangular to ellipsoidal	Absent	Short	Isodiametric sclereids	Isodiametric sclereids	Isodiametric sclereids	Present	Transseptal, central	Ventral
Nyssaceae											
<i>Nyssa sylvatica</i>	Extant	1–(2)	Ellipsoidal	Absent	Short	Fibers	Fibers	Fibers	Present	Transseptal	Ventral
<i>Nyssa spatulata</i>	Eocene	3	Crescent-shaped	Present	Short	Fibers	Fibers	Fibers	?	Transseptal	?
<i>Campiotheca acuminata</i>	Extant	1	Ellipsoidal	Absent	Short	Fibers	Fibers	Fibers	Absent	Transseptal	?

(Continues)

TABLE 1 (Continued)

Taxon	Age	Locule no./fruit	Locule shape in XS	Exterior ridge(s) on valve	Valve length	Septum histology	Histology of central axis	Valve histology	Inner endocarp*	Endocarp vasculature	Raphe position
Davidiaceae											
<i>Davidia antiqua</i>	Paleocene	6–8	Subtriangular	Absent	Elongate	Fibers	Fibers	Fibers	?	Longitudinal rows in septa	Ventral
<i>Davidia involucreata</i>	Extant	6+	Subtriangular	Present	Elongate	Elongate sclereids, fibers	Fibers	Fibers	Present	Longitudinal rows in septa	Ventral
Mastixiaceae											
<i>Mastixia pentandra</i>	Extant	1	Crescent-shaped	Absent	Elongate	Fibers	Fibers	Fibers	Absent	Transseptal	Ventral
<i>Diplopanax stachyanthus</i>	Extant	1	Crescent-shaped	Absent	Elongate	Fibers	Fibers	Fibers	Present	Longitudinal rows in septa	?
<i>Retinomastixia schultei</i>	Miocene	1	Crescent-shaped	Absent	Elongate	Fibers & resin canals	Fibers & resin canals	Fibers & resin canals	Absent	Transseptal	Ventral
Cornaceae											
<i>Cornus oblonga</i>	Extant	3–(4)	Ellipsoidal	Present	Elongate	Isodiametric sclereids	Isodiametric sclereids	Isodiametric sclereids	Absent	Transseptal	Lateral/dorsal
<i>Cornus clarnensis</i>	Eocene	3	Ellipsoidal	Absent	Elongate	Isodiametric sclereids	Isodiametric sclereids	Isodiametric sclereids	Absent	Transseptal	?
<i>Cornus multilocularis</i>	Eocene	3–6	Subtriangular	Absent	Elongate	Elongate sclereids, secretory cavities	Elongate sclereids, secretory cavities	Isodiametric sclereids, secretory cavities	Present	Transseptal	Lateral/dorsal
Alangiaceae											
<i>Alangium chinense</i>	Extant	2	Ellipsoidal	Absent	Elongate	Isodiametric sclereids, parenchyma	Isodiametric sclereids, parenchyma	Isodiametric sclereids	Absent	Transseptal	Lateral/dorsal
<i>Alangium vermontanum</i>	Miocene	2	Ellipsoidal	Absent	Elongate	Isodiametric sclereids, parenchyma	Isodiametric sclereids, parenchyma	Isodiametric sclereids	Absent	Transseptal	?
Curtisiaceae											
<i>Curtisia dentata</i>	Extant	4	Subtriangular	Absent	Elongate	Isodiametric sclereids	Vascular tissue, isodiametric sclereids	Isodiametric sclereids	Absent	Central in fruit axis	Ventral

TABLE 1 (Continued)

Taxon	Age	Locule no./fruit	Locule shape in XS	Exterior ridge(s) on valve	Valve length	Septum histology	Histology of central axis	Valve histology	Inner endocarp*	Endocarp vasculature	Raphe position
<i>Curtisia quadrilocularis</i>	Eocene	4	Subtriangular	Absent	Elongate	Isodiametric sclereids	Vascular tissue, isodiametric sclereids	Isodiametric sclereids	Absent	Central in fruit axis	Ventral
Grubbiaceae											
<i>Grubbia tomentosa</i>	Extant	1	Ellipsoidal	Valves absent	Absent	Isodiametric sclereids	Vascular tissue, isodiametric sclereids	Valves absent	?	Central in fruit axis	Ventral
<i>Operculifructus lopezii</i>	Campanian	1	Ellipsoidal	Valves absent	Absent	Elongate sclereids	Vascular tissue, elongate sclereids	Valves absent	Absent	Central in fruit axis	Ventral

Note: Data from Kirchheimer, 1938; Chandler, 1962; Eyde et al., 1969; Carlquist, 1977; Eyde, 1963, 1968, 1988; Manchester, 1994, 2002; Takahashi et al., 2002; Manchester et al., 1999, 2007, 2010, 2015; Yembaturova et al., 2009; R. Serbet, University of Kansas, personal communication, 2016; Atkinson, 2016; Hayes et al., 2018; Atkinson et al., 2018, 2019; Manchester and Collinson, 2019.

*Note: If the species has an inner endocarp, the histology of the septa, central axis, and germination valves do not include the inner endocarp.

endocarp, they have short germination valves and seeds with ventral raphes. Overall, the combination of characters that are diagnostic of the Cornaceae-Alangiaceae clade is not seen in *Fenestracarpa*, which is reflected in our phylogenetic analyses (Figures 4 and 5).

Endocarp morphology and anatomy in the NDM clade are variable (Table 1). For instance, endocarps in Mastixiaceae and Davidiaceae have elongate germination valves that run the entire length of the fruit, while those of Nyssaceae have short germination valves (except for the fossil *Browniea* Manchester & Hickey, 2007), which is similar to *Fenestracarpa*. A diagnostic trait for Mastixiaceae is crescent-shaped locules with some variations of that shape in fossils (e.g., *Langtonia bisulcata* Reid & Chandler; Manchester, 1994), which contrasts from the ellipsoidal to subtriangular locules of Davidiaceae and most Nyssaceae (Table 1). However, a few living and extinct species of *Nyssa* have crescent-shaped locules (Hammel and Zamora, 1990; Manchester, 1994). While Davidiaceae have endocarps with longitudinal rows of vascular bundles in the septa, Nyssaceae (excluding *Nyssa ogeche* Bartram & Marshall; Eyde, 1963) and most Mastixiaceae (excluding *Diplopanax* Hand.-Mazz.; Manchester and Collinson, 2019) have transseptal bundles. Despite the morphological variation in the NDM clade, potential apomorphies for this group are the absence of isodiametric sclereids and presence of fibers in the endocarp (excluding the inner endocarp, if present) (Table 2); however, endocarps of *Davidia* Baill. (Davidiaceae) may occasionally have sclereids toward the periphery of the septa (Eyde, 1963) where cells presumably run out of room to grow and elongate. *Fenestracarpa* endocarps do not contain fibers outside of the inner endocarp and the germination valves are composed of isodiametric sclereids. These differences (see Table 1 for additional differences with NDM families) and the recovered phylogenetic position of *Fenestracarpa* suggest that this extinct taxon cannot be assigned to the NDM clade or any of its respective families.

Like many other extinct cornalean genera from the Cretaceous and Paleogene, *Fenestracarpa* has a combination of characters that does not conform to a single family or major clade (e.g., Atkinson, 2016; Atkinson et al., 2017; Table 1). More specifically, *Fenestracarpa* is recovered in a clade of extinct genera with unknown family level affinities that is sister to the Curtisiaceae-Grubbiaceae group (Figures 4 and 5). As indicated by the identified apomorphies (Table 2), most taxa of this extinct clade have endocarps with an acuminate apex (when the apex is preserved and not lost), and the fruit central axis and septa have elongated sclereids. *Fenestracarpa* should therefore be compared to these Cretaceous and Paleocene extinct genera (Table 1).

Comparative morphology with extinct cornalean genera with unknown family-level affinities

Key characters that have been used to separate extinct genera are endocarp vascular pattern, histology, germination valve

TABLE 2 Selected identified apomorphies in PAUP* for cornalean clades under two different topologies. Numbers correspond to the character's number in our morphological matrix (Appendices S1 and S2). Non-overlapping apomorphies between topologies bolded. Asterisks (*) denote ambiguous apomorphies.

Tree topology	Fossil clade	NDM	Cornaceae-Alangiaceae	Curtisiaceae-Grubbiaceae
Total evidence	11. Acuminate apex 35. Elongated sclereids in septa and central axis 50. Vascular bundles in longitudinal rows in septa	30. No isodiametric sclereids in germination valves* 34. No isodiametric sclereids in septa and central axis*	21. Exterior grooves on septal/ventral area* 63. Lateral/dorsal raphe position	9. Non-elongate endocarp 18. No ridges on exterior surface of germination valves/dorsal area* 45. Vascular bundles in central axis
Constraint	11. Acuminate apex* 35. Elongated sclereids in septa and central axis	30. No isodiametric sclereids in germination valves 32. Fibers in germination valves 34. No isodiametric sclereids in septa and central axis 36. Fibers in septa and central axis 60. Leathery/dry mesocarp texture at maturity*	28. No conspicuous locule lining* 63. Lateral/dorsal raphe position*	9. Non-elongate endocarp 45. Vascular bundles in central axis

length, locule shape, and presence or absence of an inner endocarp (Manchester et al., 1999; Atkinson, 2016; Stockey et al., 2016; Atkinson et al., 2017, 2018, 2019; Table 1). Each genus has a unique combination of these characters. Differences in two or more of the above characters have generally been used to separate genera, while differences in endocarp ornamentation (presence or absence of ridges and furrows), general shapes, overall sizes, and number of locules have been used to separate species (Manchester et al., 2010; Takahashi et al., 2002; Atkinson, 2016; Atkinson et al., 2016, 2017, 2018).

Hironoia Takahashi, Crane & Manchester is a monotypic genus comprising *H. fusiformis* Takahashi, Crane & Manchester (2002) represented by fruits from the Coniacian of Japan. Like *Fenestracarpa*, *Hironoia* has three to four locules that are subtriangular to ellipsoidal in cross section, isodiametric sclereids in the germination valves, elongated sclereids in the central axis, and an inner endocarp. However, *Hironoia* differs from *Fenestracarpa* by having endocarps with elongate valves with exterior ridges and central vascular bundles (Takahashi et al., 2002).

Eydeia Stockey, Nishida & Atkinson contains three species: *E. hokkaidoensis* Stockey, Nishida & Atkinson (2016) from the Santonian of Japan, *E. vancouverensis* Atkinson, Stockey & Rothwell (2018) from the Coniacian of western North America, and *E. jerseyensis* Atkinson, Martínez & Crepet (2019) from the Turonian of eastern North America. In addition, there are fruits described in the dissertation of Serbet (1997) that likely are assignable to *Eydeia* (Drumheller Fruit 1 in the present study) but have been called *Davidia* by Manchester et al. (2015). These extinct species have yet to be recovered as a monophyletic group (Atkinson, 2018; Atkinson et al., 2019; present study). Of the three *Eydeia* species, *E. vancouverensis* and *E. hokkaidoensis* are the most dissimilar to *Fenestracarpa*. These *Eydeia* species have endocarps with elongate germination valves and longitudinal rows of vascular bundles in the septa and lack an inner endocarp, which differ considerably from the endocarps of *Fenestracarpa* (Stockey et al., 2016; Atkinson et al., 2018, 2019). Endocarps of *Eydeia jerseyensis* are similar to those of *Fenestracarpa* due to the presence of short germination valves and an inner-endocarp composed of circum-locular fibers (Atkinson et al., 2019). However, *E. jerseyensis* has an outer endocarp consisting only of isodiametric sclereids and vascular bundles in longitudinal rows in the septa, which differs from the endocarps of *Fenestracarpa* (Table 1). The differences in endocarp histology and vasculature articulated above leads us to suggest that the fruits described in this study are not assignable to *Eydeia*.

Suciacarpa Atkinson is represented by two species from the Campanian of western North America: *S. starii* Atkinson (2016) from Sucia Island and *S. xiangae* Atkinson, Stockey & Rothwell (2017) from Vancouver Island. Another Campanian fruit ("Drumheller Fruit 2" in this work) described by Serbet (1997) is most likely assignable to the genus based on phylogenetic analyses (see Atkinson, 2018;

Hayes et al., 2018; Atkinson et al., 2019; and the present study with high support); however, it was referred to as *Nyssa* by Manchester et al. (2015). Valves in *Fenestracarpa* and *Suciicarpa* are short, spanning less than half the length of their associated locules, and lack any exterior ridges, conferring a smooth endocarp surface (Table 1). However, *Suciicarpa* has crescent-shaped locules, which differ from the ellipsoidal to subtriangular locules of *Fenestracarpa*. Moreover, with the exception of Drumheller Fruit 2, *Suciicarpa* endocarps have conspicuous secretory cavities. Vascular bundles are arranged in longitudinal rows in the septa of *Suciicarpa*, while in *Fenestracarpa*, they are located in the septum periphery (Atkinson, 2016; Atkinson et al., 2017).

Obamacarpa Atkinson, Stockey & Rothwell contains one species, *Obamacarpa edenensis* Atkinson, Stockey & Rothwell (2018), from the Coniacian of western North America. *Obamacarpa* differs from *Fenestracarpa* in septum and central axis histology: *Obamacarpa* has isodiametric sclereids in the septa and central axis, whereas *Fenestracarpa* also has elongated sclereids in the outer endocarp. Additionally, *Obamacarpa* has vascular bundles in longitudinal rows in the septa (Atkinson et al., 2018).

Edencarpa Atkinson, Stockey & Rothwell contains the species *Edencarpa grandis* Atkinson, Stockey & Rothwell (2018) from the Coniacian of western North America. Unlike *Fenestracarpa*, *Edencarpa* has endocarps with elongate germination valves. Moreover, *Edencarpa* endocarps lack an inner endocarp and have bundles arranged in longitudinal rows in the septa (Atkinson et al., 2018).

Sheltercarpa Atkinson, Stockey & Rothwell has one species, *Sheltercarpa vancoverensis* Atkinson, Stockey & Rothwell (2017), from the Campanian of western North America. Both genera have short germination valves with no exterior ridges. Like *Fenestracarpa*, *Sheltercarpa* endocarps contain isodiametric and elongated sclereids in the germination valves, septa, and central axis. However, *Sheltercarpa* has a distinct locule lining and lacks an inner endocarp (Atkinson et al., 2017). Vasculature in the endocarps of *Sheltercarpa* is unknown. Due to these histological differences and uncertainty of the vasculature in *Sheltercarpa*, it is conservative to separate *Fenestracarpa* from *Sheltercarpa*.

Our phylogenetic analysis recovers *Fenestracarpa* sister to *Amersinia obtrullata* Manchester, Crane & Golovneva (1999), which is represented by permineralized fossil infructescences and leaf compressions from the Paleocene of North America and Asia. Both taxa have endocarps with short germination valves, an inner endocarp, and seeds with ventral raphes (Table 1). While vascular bundles in *Fenestracarpa* and *Amersinia* are located in the septum periphery, bundles are also present in the central axis of *Amersinia* (Manchester et al., 1999). In addition, *Amersinia* has a locule lining and an outer endocarp composed of only isodiametric sclereids, which is absent in *Fenestracarpa*. Due to these differences, we refrain from assigning the fruits of *Fenestracarpa* to *Amersinia*.

Our comparative analysis of fruit morphology indicates that *Fenestracarpa* has a combination of characters that does not conform to any currently recognized living family in the order (Table 1). Unique character combinations are typical for the majority of Cretaceous and some Paleocene cornaleans. Moreover, the fruits from this study are distinct from these extinct taxa. Therefore, we assign these newly described fruits to a new genus and species, *Fenestracarpa washingtonensis* gen. et sp. nov. Nguyen & Atkinson.

Morphological fruit and seed characters are phylogenetically informative in Cornales

Our pseudofossilization analyses indicate that fruit morphological characters can recover most taxa within the correct family or major clade with moderate to high support (i.e., most pseudofossils' shallowest well-supported nodes were within their respective major clade). Notably, four of nine pseudofossils were recovered in their original position (i.e., at the species level) as reflected in the reference tree (Figure 3). The recovered phylogenetic positions of the pseudofossils demonstrate that missing characters typical of anatomically preserved cornalean fruits do not severely impede accurate placement into their respective major clades. These results make us reasonably confident in the recovered positions of fossil taxa at the major clade and family level in our phylogenetic analyses.

Two instances of morphologically divergent taxa from clades with low diversity presented challenges in our pseudofossilization analyses (see Matsunaga and Smith, 2021, for a discussion on similar scenarios in palms). For instance, while pseudofossil *Curtisia dentata* was accurately placed in the Curtisiaceae-Grubbiaceae group, it was the only pseudofossil with its shallowest well-supported node outside of its major clade. Species diversity in the Curtisiaceae-Grubbiaceae clade is relatively low with Curtisiaceae being monotypic and Grubbiaceae consisting of three species in a single genus, *Grubbia*. The only species of Grubbiaceae sampled in this study is *Grubbia tomentosa*, which has many inapplicable and derived character scorings (e.g., absence of germination valves; presence of symplicate zone) relative to *Curtisia* and other drupaceous cornaleans. Removing *Curtisia* from the reference tree for its pseudofossilization analysis may have reduced the phylogenetic signal in the distribution of characters by removing informative characters defined by this taxon, which would make the analysis struggle to recover strong support to the pseudofossil's placement in the inferred tree (see Guillaume and Cooper, 2016; Matsunaga and Smith, 2021). In a separate example, there were inaccurate placements of pseudofossil *Diplopanax stachyanthus* (Mastixiaceae) as sister to *Davidia involucrata* (Davidiaceae) and vice versa with moderate support. Taxon sampling in Mastixiaceae was low in our analyses, and Davidiaceae is monotypic and morphologically divergent, which leads us to suspect that removing these taxa from the reference tree for their

respective pseudofossilization analysis limited informative character distributions. In addition, convergence between *Diplopanax* and *Davidia* (e.g., longitudinal rows of bundles in the septa and histological characters) likely played a significant role in their positions as pseudofossils. Importantly, despite the inaccurate terminal positions of *Diplopanax* and *Davidia* pseudofossils, they were accurately recovered in the NDM clade with high support (bootstrap support >95) (Figure 3; Appendix S5).

One could argue that the characters in our dataset are insufficient to accurately place species of morphologically divergent and monotypic genera (e.g., *Curtisia*, *Davidia*, and *Diplopanax*) at the family level and below. However, when these extant species are included in our total-evidence and fossil-inclusive constrained analyses, fossils of these genera are recovered as sister to or in positions close to living species of their respective genus. For example, the extinct *Curtisia quadrilocularis* was recovered as sister to extant *Curtisia dentata* and the Paleogene *Davidia antiqua* was placed sister to living *Davidia involucreta*. The extinct species of *Diplopanax eydei* was recovered within Mastixiaceae (Figures 4 and 5). These results highlight the importance of taxon sampling (especially for morphologically divergent extant taxa) for establishing character distributions that are informative for phylogenetic inference of fossil taxa (see Guillerme and Cooper, 2016; Matsunaga and Smith, 2021).

Inferring relationships of extinct taxa and turnover within Cornales

Cornales experienced a rapid phylogenetic diversification soon after their crown group evolved in the Late Cretaceous (Xiang et al., 2011; Atkinson, 2018; Fu et al., 2019), which is indicated by short branches along the backbone of molecular phylogenies and presents challenges to resolving relationships among major clades within the order (Fan and Xiang, 2003). However, recent molecular phylogenetic studies have made meaningful advances in resolving these relationships (Xiang et al., 2011; Fu et al., 2019; Thomas et al., 2021). A recent nuclear phylogenomic study of Cornales recovered deep-node relationships concordant with morphology reflecting a clade of drupaceous taxa that is sister to a clade of families that mostly possess dehiscent capsular fruits (Hydrostachyaceae, Hydrangeaceae, and Loasaceae) (see Thomas et al., 2021). Importantly, the morphologically concordant phylogenomic analysis of Thomas et al. (2021) and our pseudofossilization analyses support past claims that fruit morphology is systematically informative within the order (e.g., Eyde, 1963, 1988; Atkinson, 2016). The robust deep-node relationships within Cornales and results from our pseudofossilization analyses provide an opportunity to directly integrate morphological, fossil, and molecular phylogenetic evidence to further assess relationships of extinct cornaleans with reasonable confidence, which in turn allows us to uncover novel perspectives on macroevolutionary patterns within the

order that are unattainable from analyzing living taxa alone (Atkinson, 2018).

Similar to the analysis of Atkinson (2018), the current phylogenetic analyses were able to recover most extinct taxa to the living genera and/or families that they were formally assigned, often with high support (e.g., *Cornus* [cf] *piggae*, *Cornus clarnensis*, *Curtisia quadrilocularis*, *Nyssia spatulata*, *Davidia antiqua*, *Alangium eydei*). The only taxon that was recovered outside the family to which it was formally assigned was the extinct genus *Amersinia*, which had been originally assigned to Nyssaceae (Manchester et al., 1999). *Amersinia* does differ from Nyssaceae in having endocarps with central vascular bundles and no chaotically oriented fibers (Eyde, 1963; Manchester et al., 1999).

One of the most surprising results of our total-evidence and constrained analyses was the recovery of a clade consisting exclusively of extinct genera. This clade is sister to the Curtisiaceae-Grubbiaceae group; however, support is low for this sister relationship (Figures 4 and 5). More specifically, this extinct clade contains 13 species within eight extinct genera, most of which are Late Cretaceous in age. It is worth noting that *Amersinia obtrullata* is the only post-Cretaceous taxon in the extinct clade in which all occurrences of the genus are restricted to the Paleocene (Manchester et al., 1999; Huegele and Manchester, 2020). Although support for the extinct major clade is not high (Figures 4 and 5), we are reasonably confident in our results for two reasons. First, as discussed, pseudofossilization analyses indicate that our fruit morphological dataset is phylogenetically informative at the major-clade and family levels. Second, Atkinson (2018) revealed that, similar to extant major clades of drupaceous Cornales, the vast majority of taxa in the extinct clade recovered in this study formed a distinct cluster in morphospace occupation. This morphospace pattern is typical of higher clades in other plant groups (see Clark et al., 2023).

The extinct major clade identified in the current analyses was not recovered in previous morphologically focused ones (Atkinson, 2018; Atkinson et al., 2019) in which most taxa of this clade formed a paraphyletic group along the NDM stem branch. This difference is likely due to the relationships of extant taxa in our analyses being predominantly influenced by molecular data, which results in more topological stability for extant taxa and, ultimately, a different morphological character distribution across the phylogeny. The relationship of living major groups recovered in our total-evidence analysis is more similar to previous molecular based studies in which Curtisiaceae and Grubbiaceae form a major clade (Fan and Xiang, 2003; Xiang et al., 2011; Fu et al., 2019; Thomas et al., 2021) while they were recovered as polyphyletic in the initial fruit morphological analysis of Atkinson (2018) and by Atkinson et al. (2019). The main difference between relationships recovered in our total-evidence analysis and those of the recent nuclear phylogenomic analysis of Thomas et al. (2021) is the position of the NDM clade. Our total evidence analysis recovered the NDM clade as sister to all other

drupaceous cornaleans while in the analysis of Thomas et al. (2021), it was recovered as sister to the Curtisiaceae-Grubbiaceae clade. Nonetheless, when we constrained relationships to reflect those reported by Thomas et al. (2021), the extinct clade was still recovered in our analysis.

Interestingly, using the matrix from Atkinson (2018), Hayes et al. (2018) conducted a morphological and fossil-inclusive phylogenetic analysis with extant relationships constrained to reflect the topology from Xiang et al. (2011) in which drupaceous cornaleans were paraphyletic. This resulted in a similar extinct clade sister to the Curtisiaceae-Grubbiaceae clade. However, *Amersinia* and *Hironoia* were recovered in a separate clade (Hayes et al., 2018). Considering that the extinct clade, with the addition of *Amersinia* and *Hironoia*, was recovered in our total-evidence analysis and in the constrained analysis reflecting the robust deep-node relationships of Thomas et al. (2021), we favor our results.

As mentioned, the majority of taxa in the extinct major clade are Late Cretaceous in age. These include the oldest cornalean fossils reported to date (*Eydeia jerseyensis*, *Eydeia vancouverensis*, *Obamacarpa edenensis*, *Edencarpa grandis*, and *Hironoia fusiformis*), which were recovered near the Turonian-Coniacian boundary (~89.9 Ma) (Takahashi et al., 2002; Atkinson et al., 2018, 2019). The minimal age of this clade indicates that it took part in the initial radiation of crown-group Cornales during the Cretaceous. During the Cretaceous, this extinct clade diversified into at least eight genera and was quite diverse by the Santonian-Campanian, while fossil records of living major cornalean clades are scant. We posit that the extinct major clade experienced high species and generic levels of extinction across the end-Cretaceous Mass Extinction event but endured into the Paleocene as evidenced by the occurrence of *Amersinia* (Manchester et al., 1999). Ultimately, the major clade would go entirely extinct later in the Cenozoic while the crown-group diversification of extant major clades and families continued.

Our findings complement and further current understanding of angiosperm turnover in deep time. Aside from our current biodiversity crises, the end-Cretaceous Mass Extinction event is the only mass extinction that angiosperms experienced in the fossil record. This event caused high rates of species extinction (Wilf et al., 2023); however, molecular phylogenies suggest most higher clades (e.g., families, orders, and higher levels) seemed to have been resilient to this biotic catastrophe (Thompson and Ramírez-Barahona, 2023). Interestingly, our results mirror these inferred patterns in which the major clade of extinct Cornales endured the extinction event with only one genus known in the Paleocene. Although the diversity of higher clades of angiosperms is unclear, it is quite possible that at least some higher clades of angiosperms went extinct when climates experienced major fluctuations throughout the Cenozoic as seen in gymnosperms (Crisp and Cook, 2011). Further identification and phylogenetic integration of extinct higher taxa across the angiosperm phylogeny is

needed to better understand the macroevolutionary patterns that shaped the diversity of flowering plants that we see today (Sauquet and Magallón, 2018; Thompson and Ramírez-Barahona, 2023).

CONCLUSIONS

The characterization of *Fenestracarpa washingtonensis* gen. nov. et sp. nov. provides additional and meaningful data on the diversity of extinct Cornales shortly after their crown-group diversification. During the Cretaceous, the crown-group diversification of Cornales resulted in the divergence of at least one major clade that is now extinct. This major clade was quite diverse on a generic level during the Cretaceous but significantly dropped in diversity afterward with only one known genus surviving into the Paleogene (*Amersinia*) before eventually going extinct. More data are needed to resolve relationships within the clade and its relation to other major clades, but our findings suggest Cornales had higher levels of taxonomic diversity in the past.

AUTHOR CONTRIBUTIONS

B.A.A. obtained the permits to collect fossils and oversaw data collection and analysis. A.T.N. prepared specimens, did photography, and conducted phylogenetic analyses. A.T.N. and B.A.A. developed the idea of this project and wrote the manuscript together.

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DATA AVAILABILITY STATEMENT

Specimens described in this study are housed in the University of Kansas Biodiversity Institute Paleobotany

Collections in Lawrence, KS, USA. Slide accession numbers for fossil specimens are 30975-31187. The character matrix used in this study is available on MorphoBank under Project 5201 (<http://morphobank.org/permalink/?P5201>).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Cornalean fruit characters for phylogenetic analyses.

Appendix S2. Character matrix for total-evidence phylogenetic analyses.

Appendix S3. GenBank accessions for loci used in phylogenetic analyses.

Appendix S4. Cornalean fruit characters from Appendix S1 scored as missing for phylogenetic pseudofossilization analyses.

Appendix S5. Trees for pseudofossilization analyses.

Appendix S6. Matrices and inferred tree files for individual pseudofossil taxa.

Appendix S7. MrBayes block for total-evidence tree and the resulting tree.

Appendix S8. Character matrix, constraint tree, and output tree from the scaffold-based constraint analysis.

Appendix S9. Mapping of all characters across the two trees.

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